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Pleistocene faunas and
the distribution of mammals
in Southern Africa

The late Dr. Austin Roberts's address, "The Old Surviving Types of Mammals in South Africa", given to the South African Association for the Advancement of Science at Windhoek in 1937, appears to me to mark a turning-point in the study of faunal history in Southern Africa. In it he discussed the historical development of the present-day South African fauna as inferred from its distribution, without considering the limited fossil evidence then available. So far as the recent past is concerned, the volume of such evidence has increased enormously in the succeeding quarter-century; when all allowance has been made for possible synonyms, more than two hundred mammalian species can now be listed from deposits belonging to some part of the Pleistocene.

Although there is no continuous local sequence of Pleistocene deposits in South Africa comparable with that at Olduvai Gorge in East Africa, our major fossil assemblages can be arranged in a succession in which some four or five stages can be recognised by changes in the composition of the fauna. In the present state of our knowledge, such stages are best identified by local site names; the proposal made in 1955 to use East African names throughout the continent has proved premature and must perforce be abandoned.

The earliest of our faunal stages, which may be named the *Sterkfontein* stage, is typified by the main deposit at Sterkfontein and by the Limeworks site at Makapansgat; the *Australopithecus* type site at Taung probably also belongs to this stage, though its fauna displays local peculiarities. Although in the past both Taung and Sterkfontein were repeatedly claimed to be older than Pleistocene, it appears at present that they lie somewhat above the lower limit of the Pleistocene as it is now understood. The Swartkrans and Kromdraai deposits, with a number of secondary sites in the same area, represent a stage later than that of Sterkfontein; this may be named the *Swartkrans* stage. Part of the faunal assemblage from the Vaal River Younger Gravels appear to belong to the Swartkrans stage, but much of it apparently belongs to a later stage, best named, from a rich site in the north-eastern O.F.S., the *Cornelia* stage. The assemblage from the Florisbad site near Bloemfontein is in turn unquestionably later than the *Cornelia* stage; the Makapansgat Cave of Hearths deposit may prove to span the intervening period, although it appears to be mainly equivalent to Florisbad. This *Florisbad* stage may have to be divided into earlier and later phases. A further stage must be interposed between the end of the Florisbad stage and the present day, but this is not yet well characterized, as the available evidence comes from human occupation

	VAAL RIVER DEPOSITS	CAVE DEPOSITS	OPEN SITES
RECENT	"YOUNGER GRAVELS"	NUMEROUS	SITES
?		PEERS CAVE BORDER CAVE	KALKBANK
FLORISBAD STAGE		WONDERWERK MAKAPANGSAT (CAVE OF HEARTHS)	VLAKKRAAL FLORISBAD
CORNELIA STAGE			HOPEFIELD CORNELIA ? ZULULAND COAST
SWARTKRANS STAGE		BOLT'S FARM KROMDRAAI SWARTKRANS STERKFONTein EXT.	? VIRGINIA ? LANGEBAAN WEG
STERKFONTein STAGE		MAKAPANGSAT (LIMEWORKS) ? TAUNG STERKFONTein (MAIN SITE)	

Fig. 1. Sequence of recognised pleistocene faunal stages in Southern Africa, with correlation of principal sites.

sites which do not give a comprehensive picture of the fauna; it has therefore no acceptable name at present.

All the type sites and the majority of known secondary sites are concentrated in the inland plateau region. A classic site on the Zululand coast probably belongs to the Cornelia stage; in the south-west Cape there are two important sites, that at Langebaanweg provisionally assigned to the Swartkrans stage, and that near Hopefield to the end of the Cornelia stage.

Recent studies have considerably altered our earlier impression of these faunas. It is now clear that in both the Sterkfontein and the Swartkrans stages extinct species predominate. About 30 per cent of the species recorded in the Sterkfontein stage are at present tentatively identified with living forms, but experience suggests that this estimate will almost certainly prove excessive as the material becomes more completely known. In the Cornelia stage about 50 per cent of the recorded species can be fairly definitely identified as living forms; in the Florisbad stage as a whole living species constitute about 80 per cent, the remaining extinct forms being progressively eliminated during this and the succeeding stage.

Even in the Sterkfontein stage the fauna differs only slightly in general aspect from that of the present. The only truly bizarre or unexpected elements in the Pleistocene faunas are the chalicotheres, the sabre-toothed cats, and perhaps the "three-toed" horses (hipparions); all the other conspicuous extinct species, the baboons and elephants, the hypsodont pigs, the giant giraffes (sivatheres), and the numerous antelopes, are close relatives if not ancestors of existing types.

The species provisionally identified as recent in the Sterkfontein stage include many small mammals, insectivores, bats and rodents; among larger mammals are the two rhinoceroses, the hippopotamus, giraffe, Cape buffalo, eland, kudu, blue wildebeest, and impala. To these may be added in the Swartkrans stage the brown hyaena, lion, Burchell's zebra, red hartebeest, and springbok. Most of these specific identifications may however need to be revised.

In the Cornelia stage, practically all the large recent species tentatively identified in earlier stages can be recognized with much greater confidence; further additions, either definite or tentative, to the list include the Chacma baboon, spotted hyaena, quagga, warthog, black wildebeest, reedbuck, grey duiker, bloubok and sable antelope. In fact, most of the larger species appear to be present at this stage alongside of related extinct forms; the position regarding the small species is not clear, as good cave sites of this stage are lacking. Some larger recent species not at present known before the Florisbad stage, such as the vaal-ribbok and klipspringer, may be absent from deposits of the preceding stage only by chance. The most dramatic new arrival during the Florisbad stage is the African elephant, which fills a place left vacant by the extinction of the elephant species present in the Swartkrans and Cornelia stages.

It is clear that the African elephant must be regarded as an immigrant type, probably derived from west central Africa. Some other recent species which appear for the first time either in the Florisbad or the Cornelia stage may also be immigrants, but others may prove to be descended from allied species present in the Sterkfontein or Swartkrans stages.

The most striking departures from the present-day distribution of existing species are shown by the Hopefield assemblage, belonging to the end of the Cornelia stage; this includes not only the reed-buck, absent from the south-western Cape Province in historic times, but also the blue wildebeest, now essentially tropical; on the other hand, it lacks both the red hartebeest and the grey duiker, present in the same area in historic times, and identified inland during the Cornelia stage. In the inland plateau region there is evidence of a southward extension of both the tsessebe and the lechwe during the Florisbad stage if not already in the Cornelia stage. Isolated relict populations of these once more widely distributed species, or islands of species which have in fact become extinct, might conceivably have persisted into

recent times alongside of existing island or relict types. Although Roberts inferred that recent species limited to a restricted area in southern Africa, such as the mountain zebra and the vaal-ribbok, probably represented in the main an earlier faunal stratum than those with a continuous northward extension, the available fossil evidence does not warrant so simple an interpretation.

Much has been made of possible climatic fluctuations during the Pleistocene as determining factors in faunal change. The available evidence suggests that periods of diminished rainfall, even if of relatively short duration, produced more effect than increases in rainfall, although, as Roberts pointed out, the eastern part of southern Africa must always have remained wetter than the western, and so provided a refuge for types which could not readily adapt themselves to drier conditions. Roberts also justifiably inferred that dry conditions must have extended into the equatorial region at least once and probably more than once, forming a bridge or raft for the passage of species between the arid north-east and the arid south-west of Africa.

The essentially "African" aspect of the fauna of the Sterkfontein stage poses the problem of the origin of the African Pleistocene fauna as a whole. No good Pliocene faunal assemblage has yet been recovered south of the Sahara, so that the Pleistocene and recent faunas of Africa appear like the topmost twigs of trees projecting above the top of a blank wall. There are unquestionable affinities between these African faunas and the Pliocene faunas of Southern Eurasia, but these have frequently been overvalued, fostering the conception that in the later Pliocene or even early Pleistocene Africa was overrun by an Eurasian fauna. The cumulative evidence regarding the earlier Pleistocene faunas of Africa rather indicates that the continent must have been faunally autonomous throughout the Pliocene, and that African mammals migrated outwards into Eurasia both before and during the Pleistocene.

DISCUSSION

Prof. v. Zinderen Bakker: Were there indications of a more tropical fauna than at present at Hopefield? And at Langebaan?

Prof. Wells: The Langebaan evidence is insufficient for generalizations, but the first impressions at Hopefield are that the fauna was of a more tropical type than at present.

Prof. Balinsky: Large mammals have such a wide range of temperature tolerance that they may not be good indicators of climate.

Prof. Wells: That is so; I have had to point this out to my colleagues in Europe in connection with the hippopotamus.

Dr. McNae: Most of the animals to which Prof. Wells refers are browsers rather than grazers. This tends to support my previous suggestion on the artificiality of the savanna.

Dr. Bigalke: Which species does Dr. McNae classify as browsers?

Dr. McNae: Giraffe and Blue Wildebeest.

Dr. Bigalke: I do not agree that the Blue Wildebeest is a browser. Several tropical species, including this wildebeest are known historically from Kuruman and other places in the northern Cape where they do not occur today. But the gap between there and Hopefield is certainly a wide one.

Prof. Wells: They may have come via the east coast.

Dr. Poynton: Many tropical forms have a remarkable tendency to come as far south as the Vaal and to extend along the valley to the northern Cape.